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HOST ALTERNATION: A NEWLY DISCOVERED ATTRIBUTE OF THE PHYLLOXERIDAE (HOMOPTERA: APHIDOIDEA)

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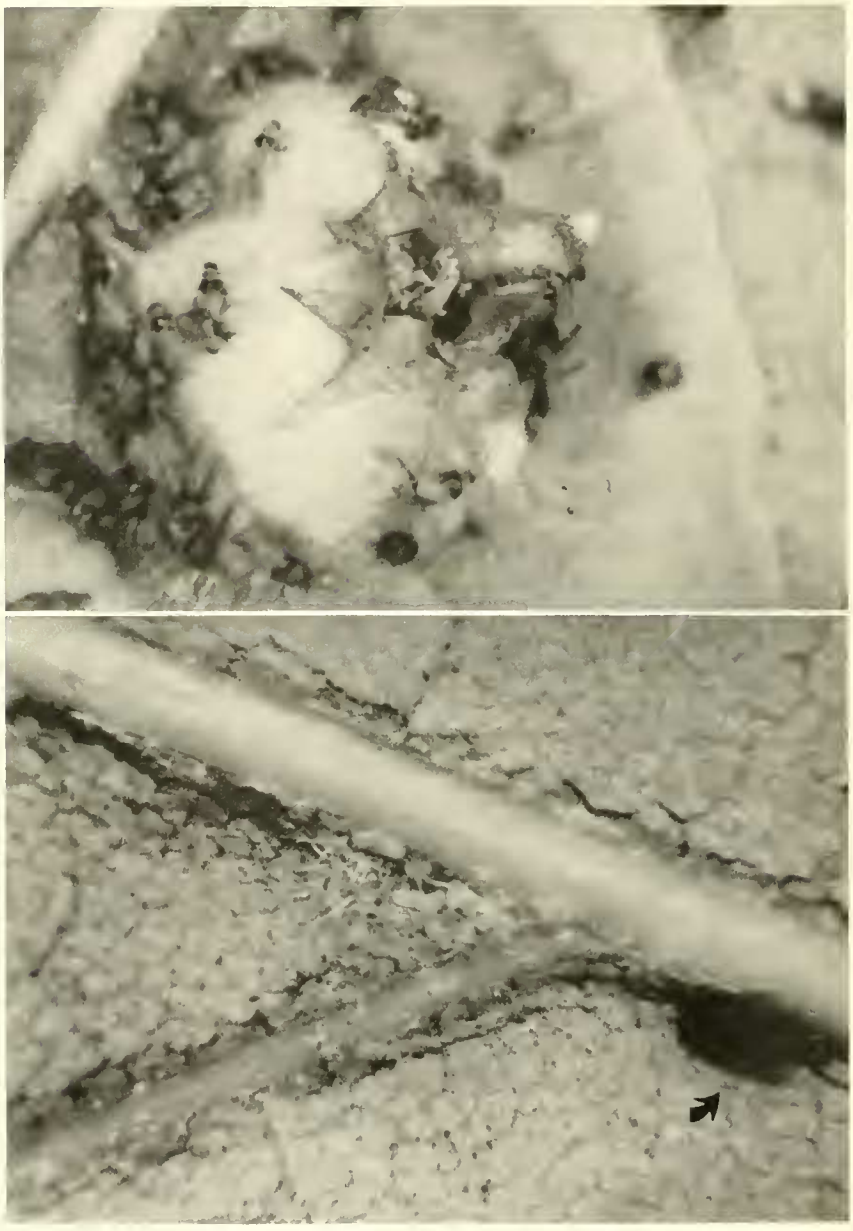
Abstract.—This is the first report of host alternation in the Phylloxeridae from one plant family (Juglandaceae) to another (Fagaceae). A six-year study of *Phylloxera* indicates that *P. texana* Stoetzel and *P. castanea* Pergande exhibit host alternation in their life cycles. In these species of *Phylloxera, Carya* (hickory) is the primary host with the secondary host being a species of *Quercus* (oak) or *Castanea* (chestnut). The Phylloxeridae, Aphididae (aphids), and Adelgidae (adelgids) constitute the superfamily Aphidoidea (Homoptera); and host alternation from one plant genus or family to another is well established in the Aphididae and Adelgidae. However, host alternation from one plant genus or family to another has not been reported or even suspected previously in the Phylloxeridae.

This paper reports for the first time the existence of host alternation in the Phylloxeridae from one plant family (Juglandaceae) to another (Fagaceae). The Phylloxeridae, Aphididae (aphids), and Adelgidae (adelgids) constitute the superfamily Aphidoidea (Homoptera); and host alternation from one plant genus or family to another is well established in the Aphididae and Adelgidae. Eastop (1966) reported that in Europe *Phylloxera florentina* Targioni-Tozzetti alternates between *Quercus ilex* and *Q. robur*, but host alternation from one plant genus or family to another has not been reported or even suspected previously in the Phylloxeridae.

From 1978 to 1984, I conducted a detailed study of the biology and morphology of species of *Phylloxera* on *Carya illinoiensis* (Wang.) K. Koch. (pecan) in Georgia, Louisiana, Oklahoma, and Texas (Stoetzel, 1981). During the study, I followed the development of the life stages from overwintering egg to overwintering egg for three gall-producing species that spend their entire life cycles on pecan in the United States; namely, *Phylloxera devastatrix* Pergande, *Phylloxera notabilis* Pergande, and *Phylloxera russellae* Stoetzel. I also observed a fourth species, *Phylloxera texana* Stoetzel, which exhibited a different developmental cycle.

In the spring, *P. texana* produced galls on pecan leaves; alate females escaped from the galls (Fig. 1), but further development on pecan was not observed, and overwintering eggs were never found. In an attempt to collect eggs, several hundred alate females of *P. texana* were collected from leaf galls and were isolated in small dishes. Only rarely did a female lay an egg, and no eggs hatched. Currently, *P. texana* is known only from the Texas counties of Brazos, Brown, and Menard.

In mid-May 1982 I studied populations of *P. texana* on pecan in Texas. When I isolated alate females from leaf galls in dishes with moistened filter paper or



Figs. 1–2. 1 (top), Alate females of *Phylloxera texana* escaping from gall on pecan leaf. 2 (bottom), Alate female of *Phyloloxera texana*, at arrow, with eggs and first instar nymphs in the tufts of hairs at the intersection of a secondary vein with the midvein on the lower surface of an oak leaf.

with newly formed pecan leaves or with pecan stems, the females died without laying eggs. When I put alate females from leaf galls in containers with leaves from *Quercus falcata* Michx. or *Q. virginiana* Mill., they readily laid many eggs that hatched into feeding first instar nymphs. An intensive check of the leaves of oak trees in the vicinity of the pecan trees resulted in the collection of alate females

of *P. texana* laying eggs in the tufts of hairs at the intersections of the secondary veins with the midvein on the lower surface of the oak leaves (Fig. 2). By late May immature stages and a few adult apterous females were found on oak leaves. Development continued on oak with the production of both alate and apterous females were found on oak leaves. Development continued on oak with the production of both alate and apterous females in June. Based on my experience with and knowledge of the developmental cycles of other species of *Phylloxera,* I predict that alate females of *P. texana* return to pecan in the fall and lay eggs that develop into sexual males and females (oviparae), and that, after mating, a sexual female will produce one overwintering egg. My attempts to establish greenhouse colonies of *P. texana* have been unsuccessful; and, since I have not been in Texas during the months of September and October, I have been unable to observe field populations in the fall.

From 1979 to 1984, I studied species of *Phylloxera* on chestnut (*Castanea dentata* (Marsh.) Borkh., *C. mollissima* Blume) and oak (*Quercus alba* L., *Q. palustris* Muenchh.) samples sent to me from West Virginia. From January to June of 1980, I was not able to find overwintering eggs on samples of twigs or branches of either chestnut or oak. The first phylloxerans I observed in samples from these trees were found in early June on the leaves, and they were alate females laying eggs that hatched into feeding first instar nymphs. Several overlapping generations of alate and apterous females were produced throughout the summer months and into September and October when the leaves began to senesce and fall from the trees. No males or overwintering eggs were collected from chestnut or oak; and only one oviparous female was collected, in October 1980, from chestnut. In June 1981 I spent a week in Frametown, West Virginia, looking for overwintering eggs and early developmental forms of phylloxerans on chestnut trees. The first life stage encountered on chestnut leaves were alate females which laid many eggs that hatched into feeding first instar nymphs. During this same period, I collected galls of an undescribed *Phylloxera* from three hickory trees, *Carya tomentosa* (Poir.) Nutt., bordering one of the nurseries containing the chestnut seedlings; and I discovered that the alate females escaping from galls on the hickory trees appeared to be identical, morphologically, with the alate females I was collecting from chestnut leaves. In late September 1981 I again spent a week in West Virginia working in the same chestnut nurseries. I found no sexual forms on the chestnut trees, but I did find solitary alate females laying eggs that were producing sexual males and females on the hickory trees. Overwintering eggs were also found on these hickory trees.

In March 1982, 1–2 year old bare-rooted seedlings of *Carya glabra, C. tomentosa, Castanea dentata, C. mollissima, Quercus alba,* and *Q. palustris* were fumigated, planted, and held in a greenhouse for transfer work. In June 1982, pots containing these six plants plus *Rosa* 'Forever Yours' were isolated in 6 cages with 32 × 32 mesh screen. I received samples of leaf galls from one of the *Carya tomentosa* bordering the chestnut nursery near Frametown, West Virginia; and I put these samples into 4 of the 6 cages with the test trees. Additionally, leaf galls were put into a small, isolated greenhouse far removed from the other plants and in which I had put two *Quercus alba,* two *Q. palustris,* four *Castanea dentata,* and four *C. mollissima.* By July it was clearly evident that no phylloxerans were on the *Carya, Quercus,* or *Rosa* plants in any of the six cages or in the isolated

greenhouse. However, large populations of phylloxerans had developed and were causing discoloration along the veins of the leaves on the chestnuts in the four cages and on all of the leaves of the chestnuts in the isolated greenhouse into which leaf galls from the hickory tree had been placed. None of the chestnut plants outside the cages in the large greenhouse had any phylloxerans on them. In September 1982, I tried to transfer alate females from *Castanea* back to *Carya*, but the transfers were unsuccessful. I conclude that the hickories, for one reason or another, were not acceptable to the phylloxerans. Hickory trees are slow bearing, and I have been unable to obtain nuts from the trees in West Virginia. During 1983 I did not find even one phylloxeran on the 8 chestnut plants in the isolated greenhouse or on the 8 caged chestnut plants in the large greenhouse. The plants survived over winter, leafed out in the spring, and continued to do well throughout 1983 and again in 1984. The phylloxeran population had been very heavy on all of these chestnuts during 1982; and, if sexual males and females and overwintering eggs had been produced, there should have been enough produced to have carried the population into 1983.

This six-year study of *Phylloxera* populations indicates that *P. texana* and *P. castanea* exhibit host alternation. I maintain that in these species of *Phylloxera*, *Carya* (hickory) is the primary host with the secondary host being a species of *Quercus* (oak) or *Castanea* (chestnut).

In North America, only *Phylloxera castanea* has been reported from *Castanea*, eight species of *Phylloxera* have been reported from *Quercus*, and approximately 50 species of *Phylloxera* have been reported from *Carya* (Haldeman, 1850; Riley, 1874; Pergande, 1904; Ferris, 1919; Duncan, 1922). Only by doing host transfers from *Carya* to *Quercus* and/or *Castanea* and back to *Carya* will it be possible to show relationships of species and to determine which specific names are valid.

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